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A NEW DESERT SUBSPECIES OF *COLIAS OCCIDENTALIS* (PIERIDAE) FROM SOUTHEASTERN OREGON

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ABSTRACT. *Colias occidentalis* Scudder is a complex polytypic species that is widely sympatric with the closely related *C. alexandra* W.H. Edwards throughout much of western North America. Populations of *C. occidentalis* have yellow males along the West Coast, orange males in the northern Rocky Mountains and across Canada, and mixed yellow/orange males across the Intermountain region of the Pacific Northwest. A southern isolate of these mixed populations has evolved in the northern Great Basin of southeastern Oregon, and is here described as ***Colias occidentalis sullivani*, new subspecies.** This subspecies uses an unique larval food plant, the desert bush pea (*Lathyrus rigidus* White). It has a relatively limited distribution in Harney and Malheur Counties in Oregon, but may extend into adjacent parts of Idaho and Nevada. In addition, *C. o. sullivani* is superficially very similar to the sympatric *C. alexandra*, and has been confused with that species in the past. However, the two species have different larval food plants, and specific distinctions in wing color patterns between them are outlined in the present paper.

Additional key words: *Lathyrus rigidus, Colias alexandra,* foodplants, adaptations, biogeography, variation.

The genus *Colias* belongs to the subfamily Coliadinae in the family Pieridae. The most recent monograph of the genus (Verhulst 2000) recognizes up to 85 species distributed throughout much of the world, although many of these taxa may be regarded as geographic subspecies of more widespread polytypic species. This problem of geographic variation combined with incipient or incomplete speciation is a major issue for many of the North American species, particularly for the species complex discussed in this paper.

Colias occidentalis Scudder and *C. alexandra* W.H. Edwards are closely related legume-feeders that are widely sympatric in western North America, and have been the focus of much taxonomic confusion in the past. Ferris (1993) has provided the most recent review of this group. Typical forms of *C. occidentalis* such as *C. o. occidentalis* and *C. o. chrysomelas* W.H. Edwards, have males colored yellow dorsally with no ultraviolet reflectance, and are distributed along the West Coast from northern California to British Columbia. The allopatric *christina* group has orange dorsal color with UV-reflectance, and is distributed across central Canada and through the northern Rocky Mountain region to South Dakota, Wyoming, Utah, and eastern Oregon. *Colias alexandra* has yellow dorsal color with mostly no UV-reflectance except for a deeper yellow/orange UV-reflecting patch on the dorsal hindwing. It is widely sympatric with both the orange *christina* and yellow *occidentalis* groups, and functions as a fully distinct biological species.

The primary confusion has centered on the *christina* group, which was originally classified as a separate species. Klots (1961) treated this group as geographic subspecies of *C. alexandra.* However, the widespread sympatry of the *christina* group with typical *C. alexandra* made this classification untenable (Ferris 1993). Ferris (1993) divided the *christina* group into three species based upon slight differences in male UV-reflectance patterns and female color patterns, including (1) *C. christina* W.H. Edwards across Canada and in the northern Rocky Mountains south to Wyoming , (2) *C. pseudochristina* Ferris in Utah and the eastern Pacific Northwest, and (3) *C. krauthii* Klots, disjunct between the Black Hills of South Dakota and southwest Yukon and adjacent Alaska. Intergrading populations between *C. pseudochristina* and typical *C. occidentalis* in Grant County of central Oregon were already known by Ferris (1993), but he regarded this intergradation as a purely local phenomenon in arguing for separate species status for *C. occidentalis* and the various members of the *christina* group.

Recent field studies strongly challenge Ferris' classification. Layberry, Hall and Lafontaine (1998) found that the *kluanensis* Ferris subspecies of *C. krauthii* forms a complete intergrading cline with *C. christina* across the southern Yukon. Likewise, extensive field work in the Pacific Northwest and northern Rocky Mountains over the past ten years has shown that the intergradation among *C. occidentalis, C. christina,* and *C. pseudochristina* is not restricted to a local phenomenon, but forms very long, gradual clines that extend from the east slope of the Oregon Cascades eastward through central and eastern Oregon to southeastern Washington and central Idaho, and then north from Wyoming to Alberta and northeast British Columbia (Pyle 2002). Therefore, it is our opinion that dorsal

FIG. 1. Variation in *Colias occidentalis sullivani* and comparison with spring brood forms of *C. alexandra edwardsii*. **Top row,** left to right dorsal views: *C. o. sullivani,* Holotype male, yellow form; *C. o. sullivani,* Allotype female, white form; *C. a. edwardsii,* male; *C. a. edwardsii,* female. **Second row,** left to right ventral views: *C. o. sullivani* male, olive-green form; *C. o. sullivani,* female, blue-green form; *C. a. edwardsii,* male; *C. a. edwardsii,* female. **Third row,** left to right ventral views: *C. o. sullivani,* male, yellow-green form; *C. o. sullivani,* male, gray-green form with large discal spot; *C. o. sullivani,* male, yellow form; *C. o. sullivani, male,* orange form. **Bottom row,** left to right dorsal views: *C. o. sullivani,* male, yellow form with slight orange flush; *C. o. sullivani,* male, light orange form; *C. o. sullivani,* male, medium orange form; *C. o. sullivani,* male, darker orange form.

UV-reflectance patterns in males of this particular *Colias* group are not useful for the classification of species. We believe that the orange *christina* group should be treated as a geographic subspecies of *Colias occidentalis.*

A peripheral part of this broader pattern of geographic variation has been the recent discovery of a distinctive new subspecies of *C. occidentalis* in the deserts of southeastern Oregon where it co-exists in sympatry with *C. alexandra.* This new discovery is the topic of the present paper.

Colias occidentalis sullivani Hammond and McCorkle, new subspecies

Male. Forewing length 23–30 mm ($\bar{x}$ = 26 mm, n = 194). Forewing apex slightly elongate and pointed. Dorsal ground color usually yellow (95%), rarely orange (5%) of the 194 specimens examined. Black border of forewing broad with smooth inner margin and yellow veins. Small black discal spot on forewing usually present, sometimes absent. Discal spot of dorsal hindwing only faintly evident and yellow. Heavy black basal suffusion present on fore and hindwings. Ventral ground color of hindwing light to dark olive-green, varying to yellow-green or gray-green. Black scaling in medial area of ventral forewing variable, heavy to absent. Discal spot on ventral hindwing usually small and white (55%), but sometimes medium size (31%) and rarely large (14%) of the 194 specimens examined. A red or purple ring around the discal spot is variably present or absent.

Male UV-reflectance. Males are highly variable with nearly 50% showing little or no UV-reflectance on dorsal wings as in typical *C. o. occidentalis.* Others show a weak, diffuse reflectance on fore and hindwings as in *C. o. pseudochristina,* or a bright luminous patch on the hindwing as in *C. alexandra,* or bright luminous patches on both fore and hindwings as in *C. o. christina.*

Female. Forewing length 25–30 mm ($\bar{x}$ = 28 mm, n = 116). Dorsal ground color usually pure white (67%), yellowish white (29%), or rarely yellow (4%) of the 116 specimens examined. Black border of

dorsal forewing usually absent (71%), vaguely present (23%) or rarely well developed (6%) of the 116 specimens examined. Black discal spot of dorsal forewing large, round to oblong. Discal spot of dorsal hindwing pale orange to white. Ground color of ventral hindwing gray-green to blue-green. Other characters as in male.

Etymology. We name this taxon in honor of Barry Sullivan of Salem, Oregon who originally discovered this butterfly, and who has contributed greatly to our knowledge of the butterfly fauna of the Pacific Northwest by his extensive exploratory collecting.

Types. Holotype: male, Oregon, Harney County, Alvord Desert Road at north end of Steens Mountains, T29S, R36E, sec.25,26; 9 May 2001, Barry Sullivan leg. The holotype is deposited in the American Museum of Natural History, New York, New York, USA.

Allotype: female, same data and deposition as holotype.

Paratypes: 192 males, 116 females, and 1 gynandromorph, same locality as holotype, 22 April 1990, 3 May 2000, 9May 2001, 25 May 2001, 11 May 2002, 13 May 2002, 15 May 2002, 16 May 2002, P.C. Hammond, J. Harry, D.V. McCorkle, H. Rice, E. Runquist, B. Sullivan, and A. Warren; 1 male, 1 female, Harney Co., east slope of Stinkingwater Mts. at U.S. Hwy. 20, 10 May 2001, 24 May 2001, D.V. McCorkle; 2 females, Harney Co., U.S. Hwy. 20 nr. Drewsey, 8 June 2001, 15 May 2002, P.C. Hammond, D.V. McCorkle; 7 males, Harney Co., south end of Stinkingwater Mts. east of Crane, 16 May 2002, P.C. Hammond and D.V. McCorkle; 1 male, 1 female, Harney Co., Alvord Desert Road at Ten Cent Lake, 25 May 1950, S.G. Jewett, Jr.; 2 males, 1 female, Malheur Co. north end of Sheepshead Mts. on Hwy. 78, 16 May 2002, P.C. Hammond and D.V. McCorkle.

Disposition of paratypes as follows: one pair each to the U.S. National Museum of Natural History, the California Academy of Sciences, the Natural History Museum of Los Angeles County, and the Allyn Museum of Entomology (Sarasota) of the Florida Museum of Natural History; five pairs to the Oregon State Arthropod Collection, Oregon State University; additional paratypes are in the private collections of Paul C. Hammond (36 males, 16 females), Jack Harry (2 males, 2 females), David V. McCorkle (40 males, 34 females), Harold Rice (10 males, 6 females), Erik Runquist (6 males, 6 females), Don Severns (7 males, 2 females), Barry Sullivan (60 males, 18 females, 1 gynandromorph), Andrew D. Warren (22 males, 23 females).

DISCUSSION

Throughout the northern Great Basin and Intermountain regions of the Pacific Northwest, sympatric populations of *C. occidentalis* and *C. alexandra* exhibit sharp ecological segregation in larval foodplants. *Colias occidentalis* primarily feeds on peas (*Lathyrus* spp.) and false lupines (*Thermopsis* spp.), while *C. alexandra* feeds mostly on milk-vetches (*Astragalus* spp.) and locoweeds (*Oxytropis* spp.) (pers. obs.). All of the above genera are herbaceous legumes of the family Fabaceae. Because most species of peas and false lupines are found in moist coniferous forest and montane meadows, populations of *C. occidentalis* are usually limited to the higher mountain ranges of the West. *Colias alexandra* often flys with *C. occidentalis* in these areas, but its larvae feed on *Astragalus* growing on nearby dry, open hillsides. Previously, it was thought that *C. alexandra* alone lived on the dry, desert plains and lower mountains of the northern Great Basin and Intermountain regions where only *Astragalus* and *Oxytropis* species usually grow.

In moist forests of central and eastern Oregon and southeast Washington, the *C. o. occidentalis/pseudochristina* intergrade populations have been observed to oviposit on *Lathyrus lanszwertii* Kell., *L. pauciflorus* Fern., and *L. nevadensis* Wats., all forest peas with a vine-type growth habit, and also on false lupine (*Thermopsis montana* Nutt.). However, there is a desert bush pea (*Lathyrus rigidus* White) that is found in the lowland sagebrush/bunchgrass steppes of central and eastern Oregon, extending into Adams County, Idaho, Washoe County, Nevada, and Modoc County, California.

On 22 April 1990, Barry Sullivan found a population of *Colias* at the north end of the Steens Mountains in Harney County, Oregon that was associated with *Lathyrus rigidus* rather than *Astragalus*. Males are mostly yellow dorsally, and have a dark olive-green ventral hindwing with a very small white discal spot that often lacks a red ring. This population was initially thought to be a peculiar form of the spring brood of *C. alexandra edwardsii* W.H. Edwards because of these characters. Two specimens of this *Colias* were first collected in this area at Ten Cent Lake by Stanley G. Jewett, Jr. on 25 May 1950, but remained identified as *C. alexandra* in the Oregon State University collection for 50 years. In May of 2000 and 2001, Barry Sullivan and DVM visited this site and noticed aspects of this *Colias* that are more similar to *C. occidentalis* than to *C. alexandra*. These include the *Lathyrus* hostplant association and the fact that nearly all females in the population are albinistic. Indeed, most females are pure white to creamy white in dorsal color, and the black wing borders are usually greatly reduced or completely absent. Female albinism is relatively rare in the sympatric *C. alexandra edwardsii*.

Additional study revealed a number of subtle wing pattern differences that distinguish this new *Colias* from *C. alexandra*, even though both species fly together at most localities. In males of *C. o. sullivani:* (1) the dorsal black wing border is usually broad with a smooth inner margin, (2) there is heavy black basal suffusion, (3) a deeper yellow/orange patch is usually absent from the dorsal hindwing, (4) the ventral hindwing ground color is a dark olive-green, and (5) some specimens have a large red-ringed ventral discal spot. The ventral ground color of females varys from gray-green to blue-green. By contrast, males of *C. alexandra* usually have: (1) a narrow black wing border, often with a dentate inner margin, (2) very little black basal suffusion, (3) a deeper yellow/orange patch on the dorsal hindwing, (4) a ventral hindwing ground color varying from gray to gray-green, and (5) a ventral discal

spot that is usually small to very small. Female ventral ground color is also gray to gray-green.

Of particular interest was the discovery that a small proportion (5%) of *C. o. sullivani* males from the type locality have orange dorsal coloration on both fore and hindwings as in the *christina/pseudochristina* forms. Except for the strange olive-green to blue-green ventral ground color, all of the differences that distinguish this new *Colias* from *C. alexandra* are also shared by other races of *C. occidentalis*, including a high frequency of female albinism. Figure 1 illustrates these variations in *C. o. sullivani* and the differences from *C. alexandra*.

During May of 2001 and 2002, major efforts were made to locate additional populations of this new *Colias* using OSU herbarium records of *Lathyrus rigidus* as a guide. Extensive populations of the bush pea were indeed located in the John Day valley of Grant County and the Powder River valley in Union and Baker Counties on dry, open prairie. However, these areas are within the general range of forest *C. o. occidentalis/pseudochristina* populations, and these apparently never associate with the lowland *L. rigidus*. At the southwest edge of the Wallowa Mountains in Union County, dry open hills covered with *L. rigidus* are present at a forest/prairie ecotone where *L. nevadensis* and *L. pauciflorus* occur in forest riparian areas along a stream. One apparently stray male of *C. o. pseudochristina* was collected on the open hillside among the *L. rigidus*, but we have no further evidence that this subspecies uses *L. rigidus* at this site.

However, additional populations of *C. o. sullivani* were located in Harney and Malheur Counties. This part of southeastern Oregon covers a diverse landscape of desert mountain ranges, lowland plains, and rugged canyonlands. The bush pea was found to be quite local and narrowly restricted in habitat, but was often extremely abundant, especially in areas that had evidence of past fires. The habitat consists of low hillsides just above the valley floor. Peas were never found on the lowland plains proper or higher in the mountains. Vegetation in the habitat is usually a sagebrush/bunchgrass prairie, although at the type locality, the ground is somewhat barren of vegetation except for the pea plants and a rich variety of native herbs.

Several thousand butterflies were present at the type locality during 2002, with the adults flying low among the peas. At all other sites observed, the butterflies were only moderately abundant to very rare. Nectaring usually takes place from the pea flowers or from composites. Many ova and young larvae were collected from pea plants during May of 2001 and 2002. The adult flight season lasts from late April to early June, and there is only a single generation per year. Pea plants enter senescence by June, so reproductive efforts must be complete by that time.

At the time of this writing, Malheur County is mostly unexplored for *C. o. sullivani*, but herbarium records indicate that extensive populations of *L. rigidus* are present in central parts of the county west of the Owyhee River. It is possible that the butterfly could occur eastward into Owyhee County, Idaho. Also, the Bowden Hills and Trout Creek Mountains in southern Harney and Malheur Counties remain unexplored. However, a small population of *C. o. sullivani* was located at the north end of the Sheepshead Mountains about 16 km east of the type locality.

In the northeast corner of Harney County, additional populations of *C. o. sullivani* were located along the eastern edge of the Stinkingwater Mountains, both east of Stinkingwater Pass on U.S. Highway 20 and at the south end of the mountains east of Crane. Indeed, populations are probably located along the entire eastern edge of these mountains. More butterflies were found to the east near Drewsey on Highway 20, and it is probable that populations are scattered throughout central Malheur County south of Juntura, but access to many areas is limited.

However, a particularly important population was located north of Juntura and east of Beulah Reservoir in northwestern Malheur County near the prairie/forest ecotone not far from the southeast edge of the Blue Mountains. This population is still basically of the *C. o. sullivani* type, and is associated with a very large population of *L. rigidus* on a bunchgrass/sagebrush prairie in a mid-elevation valley. Here the frequency of dorsally orange males of the *christina/pseudochristina* type is much higher, around 22% compared to 5% at the type locality about 112 km to the south. The frequency of medium to large discal spots on the ventral hindwing is also much higher, about 78% compared to 45% at the type locality. Also, about 9% have a yellow or orange ground color on the ventral hindwing instead of the greenish color characteristic of *C. o.sullivani*. These character frequencies suggest extensive gene exchange with the *C. o. pseudochristina* forest populations to the north in the Blue Mountains.

In conclusion, it is hypothesized that *C. o. sullivani* probably evolved from the *C. o. occidentalis/pseudochristina* populations in the Blue Mountains, and that ancestral populations spread southward from the Blue Mountains into the Steens Mountains during a glacial maxima of the Pleistocene, following the forest habitat of *Thermopsis* and *Lathyrus nevadensis* southward. As conditions warmed and dried during an interglacial period, the ancestral butterfly probably dwindled and

nearly disappeared along with its forest foodplants in the Steens Mountains, except for a small founder population that was able to switch and adapt to *Lathyrus rigidus*. *Colias o. sullivani* appears to be highly adapted for feeding on this particular foodplant, while the northern populations of *C. occidentalis* in the Blue Mountains seem largely unable to switch to *L. rigidus* even when it is locally available at the prairie/forest ecotone. Moreover, the olive-green to blue-green ground color of the ventral hindwing of *C. o. sullivani* blends perfectly in camouflage with the blue-green foliage of the hostplant.

One other line of evidence in support of the above evolutionary speculations comes from a large population of the *C. o. occidentalis/pseudochristina* intergrade type in the Aldrich Mountains of Grant County. A sample of 276 males showed a frequency of 70% dorsal yellow color and 30% orange color. However, on the ventral hindwing, the ground color was 66% orange, 29% yellow, and 5% green, while discal spot size was 27% large, 44% medium, and 29% small. Likewise, a sample of 43 females from the same population showed a dorsal ground color of 19% orange, 37% yellow, 30% yellowish white, and 14% pure white, while the black wing border was heavily developed in 16%, slightly present in 42%, and completely absent in 42%. Thus, a few male and female individuals from this northern population are nearly a perfect match in color phenotype to *C. o. sullivani*.

In addition, it should be noted that male UV-reflectance patterns in *C. o. sullivani* show the same range of polymorphic variation as in the *C. o. occidentalis/pseudochristina* intergrade populations from Grant County, Oregon illustrated by Ferris (1993). Approximately 50% of males show no UV-reflectance as in typical *C. o. occidentalis*, while others show a weak, diffuse reflectance as in *C. o. pseudochristina*, or a bright luminous patch on the hindwing as in *C. alexandra*, or bright luminous patches on both the fore and hindwings as in *C. o. christina*. Thus it appears that most genetic traits used in the evolution of this desert subspecies were originally present at low frequencies in the ancestral forest populations.

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